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Original Article

Evidence for nonconsumptive effects from a large predator in an ungulate prey?

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Predators can indirectly affect prey survival and reproduction by evoking costly antipredator responses. Such nonconsumptive effects may be as strong or stronger than consumptive predator effects. However, evidence for this in large terrestrial vertebrate systems is equivocal and few studies quantify the actual fitness costs of nonconsumptive effects. Here, we investigated whether nonconsumptive effects elicited by Eurasian lynx (*Lynx lynx*), a large terrestrial predator, reduced survival in an ungulate prey, the European roe deer (*Capreolus capreolus*). To reveal the behavioral processes underlying nonconsumptive effects, we distinguished between proactive risk avoidance of areas with high lynx encounter probability, and reactive risk avoidance in response to actual lynx encounters and analyzed these responses using step selection functions. We also quantified the consequences of these behaviors for deer survival. Deer reacted differently at day and at night, but avoided high-risk areas proactively during the day and at night in the summer. During a predator encounter, deer increased avoidance of high-risk areas at night but not during the day. Thus, roe deer exhibited a behavioral response race that involved temporally and spatially varying tradeoffs with environmental constraints. We found evidence that nonconsumptive effects of lynx predation risk reduced deer survival and that survival was more sensitive to variation in nonconsumptive effects of lynx than to variation in human proximity. Our findings highlight that nonconsumptive effects may depend on the spatiotemporal distribution of risks and the environmental context, and we discuss how human factors contribute to predator–prey dynamics in human dominated landscapes.

Key words: **Carnivores, predator–prey interactions, survival analysis, trophic interactions.**

INTRODUCTION

The ecology of fear framework predicts that fearful prey will respond to the presence of predators in order to reduce their exposure to predation risk (Brown et al. 1999). Such behavioral responses to predator presence often come at the cost of reduced feeding rates, changes in diet or increased stress levels, which can alter prey survival and reproduction (Lima and Dill 1990; Boonstra et al. 1998; Lima 1998). An increasing body of literature shows that such nonconsumptive effects of predators are important in shaping population dynamics of prey species and may even outweigh the consumptive effects in the long run (reviewed in Brown and Kotler 2004; Preisser et al. 2005; Peckarsky et al. 2008). While the bulk of this evidence comes from experimental aquatic or invertebrate systems, several studies of wild terrestrial mammal populations have also found marked behavioral responses of prey to predator presence (e.g., Fortin et al. 2005; Thaker et al. 2011; reviewed in Clinchy et al. 2013; Creel et al. 2014). Nonetheless, only few studies have looked at large mammal predator–prey systems where the evidence of demographic costs from nonconsumptive effects is controversial (Creel et al. 2007; Christianson and Creel 2010; Creel 2011; Middleton et al. 2013 but see MacLeod et al. 2017). Assessing the importance of risk effects on prey population dynamics requires establishing a link between the presence of a predator and the behavioral response in the prey with the demographic costs for the prey (Creel 2011). Thus, in order to move toward a conceptual framework predicting how risk effects affect prey population dynamics in large mammal systems, studies are needed that investigate the mechanisms causing nonconsumptive effects and link their costs to reductions in survival and reproduction (Creel et al. 2008; Creel et al. 2011; MacLeod et al. 2017).

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Nonconsumptive effects refer to behavioral changes in prey to reduce the risk of predation (e.g., Preisser et al. 2007). Predation risk varies both in space and time. Spatial variation in risk is a function of predator habitat selection and specific habitat features that modify attack success. Temporal variation in predation risk depends on predator space use (presence or absence) and on external factors such as light conditions or snow cover, which may change the success rate of predators (Lima and Dill 1990). The ecology of fear framework assumes that prey individuals have some information about this spatial and temporal variation in predation risk and may change their behavior in response to it (Brown et al. 1999). For example, prey may prevent exposure to high predation risk by increasing vigilance (Laundre et al. 2001; Creel et al. 2014), reducing activity (Kotler et al. 1992; Griffin et al. 2005), avoiding the preferred habitat of predators (Hebblewhite et al. 2005; Atwood et al. 2009), or by moving into safe habitat where the probability of being killed given an encounter is reduced (Thaker et al. 2011). Two hypotheses have been proposed to explain how prey respond to temporal and spatial variation in predation risk (Creel et al. 2008): First, the *risky places hypothesis* predicts that prey assess spatial variation in predation risk proactively by the long term level of risk based on indirect cues associated with particular habitat features. The assessment of the long-term level of risk may be temporally dynamic, e.g., prey may only avoid risky areas during activity peaks of the predator (Kotler et al. 2002). Second, the *risky times hypothesis* predicts that prey will respond reactively to temporal variation in predation risk as a function of direct cues of predator presence or absence. Proactive and reactive responses to predation risk are not mutually exclusive and studies have found evidence for both (e.g., Fortin et al. 2005 for response of elk to long term predation risk by wolves, Courbin et al. 2016 for response of zebras to encounter with lions), yet the 2 responses are only rarely considered concurrently (but see Valeix et al. 2009; Creel et al. 2014).

Responses of prey to predation risk do not occur in isolation. Instead, prey have to trade off risk avoidance with resource acquisition and other activities. Depending on internal and external constraints, e.g., body condition, reproductive state, food availability, weather conditions, etc., prey animals will trade off risk avoidance differently. Both theoretical (Sih 2005) and empirical evidence (e.g., Lone et al. 2016) support the notion that prey species will therefore not be able to avoid predation risk at all times and are sometimes forced to choose habitats with high predation risk, to find food, mating partners, or other essential resources.

Additional external drivers may also influence the response of prey to predation risk and how they tradeoff between different risk factors. Most terrestrial ecosystems today are human dominated landscapes and human-related causes of mortality can make up a substantial part of overall wildlife mortality in these systems (Sih et al. 2011). As a consequence, several recent studies have found animals (both predators and prey) to show strong fear responses toward humans, such as displacements to less disturbed habitat types or shifts in activity patterns toward time periods of lower human activity (e.g., Ordiz et al. 2012; Lone et al. 2016; Gehr et al. 2017a; Gehr et al. 2017b). Such responses to human disturbance may have similar indirect effects on demography of wild populations as nonconsumptive effects due to natural predators (Ciuti et al. 2012). It is crucial therefore to account for the role of human disturbance in studies of nonconsumptive effects in human dominated landscapes.

In this study, we investigated proactive and reactive antipredator responses and their interaction in shaping nonconsumptive effects elicited by a large mammalian predator in a human dominated landscape, and we asked if these effects were strong enough to translate into reduced survival. Specifically, we tested if deer show a general avoidance of areas with increased lynx encounter probability (showing a proactive response to risky places) and whether their avoidance behavior changes after an actual lynx encounter (the reactive response to risky times). Because roe deer territories are small we expected the reactive response to a lynx encounter to occur at small spatial scales through changes in the avoidance of risky places rather than through large scale movements away from an encounter site. In addition to this increased avoidance of risky places during risky times, we also expected deer to reduce their movement rates in order to evade detection by lynx, an antipredator behavior known from small mammalian prey species (e.g., Kotler et al. 1992). Finally, we tested whether nonconsumptive effects elicited by lynx can be strong enough to affect roe deer survival. To do so, we analyzed whether deer living in more risky places suffered from higher nonlynx mortality than deer from less risky places. We thereby assumed that deer living in an area with a high risk exposure suffered from increased nonconsumptive effects such as higher investment into antipredator behavior or prolonged stress responses with resulting negative effects on survival. To put the relative importance of these effects in perspective, we compared the nonconsumptive effects of lynx to the direct and indirect effects of humans on roe deer mortality.

In summary, we tested the following 4 predictions: 1) Roe deer proactively avoid areas of high chronic lynx predation risk according to the risky places hypothesis. 2) Roe deer increase their avoidance of high risk areas during a reactive response (i.e., under acute predation risk) according to the risky times hypothesis, and 3) they reduce their movement rates in these situations. 4) These nonconsumptive effects result in reduced survival of roe deer living in areas of high chronic predation risk.

METHODS

Study area

The study area in the Swiss Alps covered ~1500 km^2 (center coordinates 46.559905 N, 7.513052 E) and ranged in altitude between 600 m and 3500 m a.s.l. Most human settlements (33 inhabitants/km^2) in the region are situated at the valley bottoms. Valley bottoms and lower slopes have been deforested since the middle ages for agricultural use. Remaining forests (about 30% of the total area) are situated mostly on the higher slopes and are highly fragmented. The entire region is used intensively for recreational purposes (Pesenti and Zimmermann 2013). Besides outdoor tourism such as hiking and skiing, hunting is an important activity among local people. The hunting season on chamois *(Rupicapra rupicapra)* and red deer (*Cervus elaphus*) lasts all of September, whereas roe deer hunting occurs between October 1 and November 15. Lynx density in the region was estimated at 2.05 independent lynx/100 km^2 from a camera-trapping census in 2013/14 (Zimmermann et al. 2014). Roe deer (36% of identified kills) and chamois (39%; KORA, unpublished data) are the main prey items of the lynx in the study area.

Animal captures and data collection

Between November 2011 and April 2013 roe deer aged 5 months or older were captured (n = 65; 23 males and 42 females) using drive nets or box traps and then equipped with Global Positioning

System (GPS) collars (e-obs GmbH, Gruenwald, Germany) recording locations every 30 min (n = 1,351,368 locations between November 2011 and March 2015). Because mean GPS error (27 m) was large with respect to the mean step length of 54 m at a 30-min interval (Visscher 2006), data were rarefied to 2 h fix intervals resulting in a data set with 338,942 deer locations (mean step length = 123 m). To obtain independent estimates of predation risk, we simultaneously captured and GPS-collared 15 lynx (8 males and 7 females) in our study area using foot snares, solid wooden box traps or a remote-controlled tele-injection system. Lynx locations were recorded on average every 3 h yielding 19,797 GPS locations of lynx between March 2011 and September 2014. The GPS error was estimated at 8.8 m (± 1.3 m SE), whereas mean step length was 615m. Capture protocol and data collection for lynx are described in detail elsewhere (Vogt et al. 2016). A detailed map including all GPS locations for lynx and roe deer are provided in Figure 1.

Measuring chronic and acute predation risk

Chronic predation risk

To characterize the proactive response of roe deer to the chronic background level of predation risk by lynx (according to the risky places hypothesis), a previously developed resource selection function (RSF) model for lynx in the study area was used (Supplementary Appendix S1 and Gehr 2016). The RSF modeled temporal dynamics in habitat selection of lynx, treating time of day and season as continuous variables (Table S1 in Supplementary Appendix S1). We used the model values at each deer location to define the chronic predation risk (Figure 2). Thus, chronic predation risk varied as a function of spatial and temporal differences in lynx habitat selection. Zimmermann et al. (2014) found that lynx occurred across our entire study area. Hence, the lynx resource selection function values at each deer location are a reasonable estimate of the long-term lynx encounter probability. In the following we refer to this as the chronic predation risk. However, the probability of being killed given an encounter is determined by additional factors (e.g., attack location, prey vigilance and vulnerability, etc.), which we could not account for in this study. To compare the risk of encountering a lynx to the probability of being killed, we contrasted 1) the mean chronic predation risk of random locations within lynx home ranges to the mean chronic predation risk of lynx locations, and 2) the mean chronic predation risk for an independently collected dataset of 199 lynx killed roe deer from our study area (noncollared deer; Gehr et al. 2017b). For the comparison among datasets we scaled predation risk to between 0 and 1, after removing the most extreme values (i.e., 0.995 quantile). Most lynx kills occur between dusk and dawn. Thus, we restricted lynx locations to nighttime and calculated chronic predation risk for kills and random locations at midnight using the time-specific lynx RSF. If our chronic predation risk measure was a good estimate of the actual risk of being killed by a lynx, we expected it to be higher for lynx locations and kill sites than for random locations.

Acute predation risk

To assess the reactive response of roe deer to the immediate presence of a lynx (acute predation risk during risky times), the combined lynx and roe deer location data were searched for incidences of acute predation risk. We restricted this analysis to lynx and deer whose 100% minimum convex polygons (MCP) overlapped (12 lynx and 58 deer with 17,164 and 316,195 locations, respectively). The

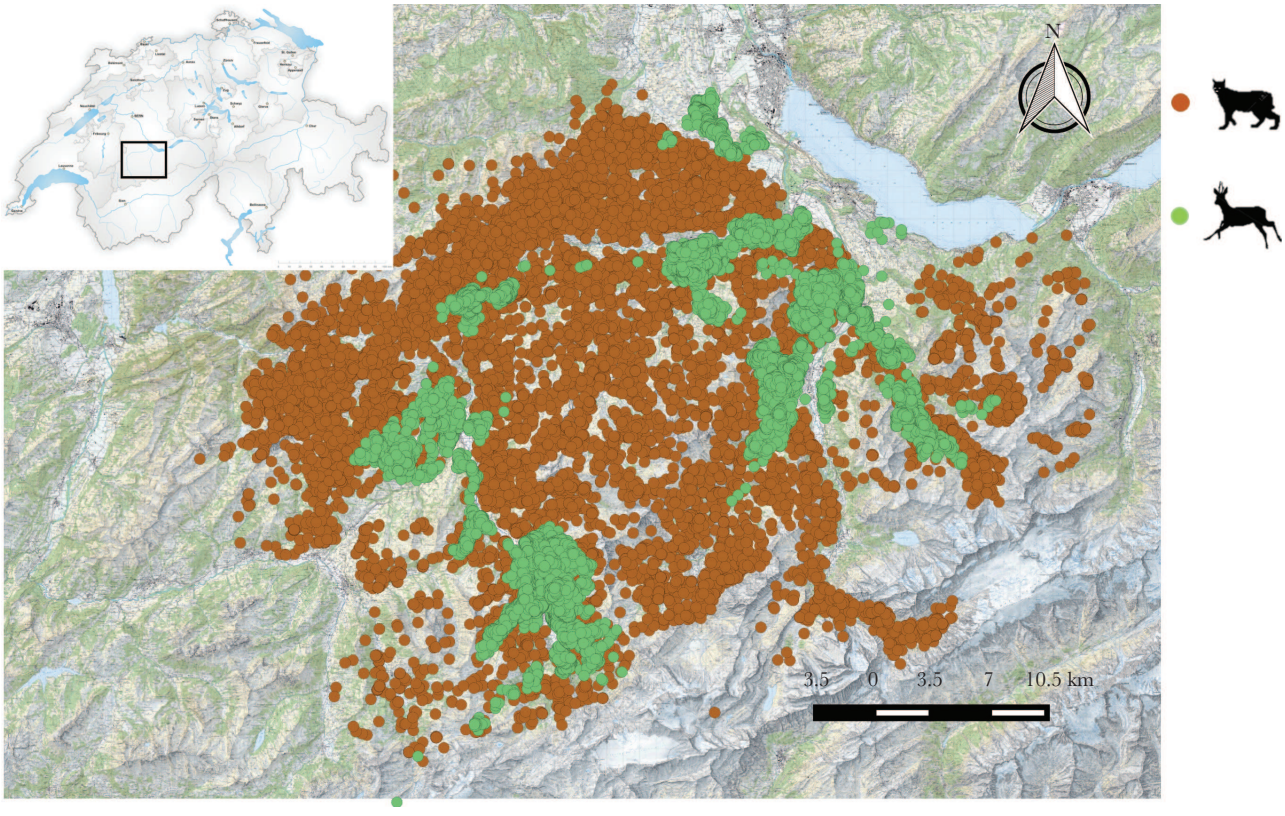

Figure 1
Map of the study site showing locations and spatial overlap of radio-collared lynx and radio-collared roe deer in this study.

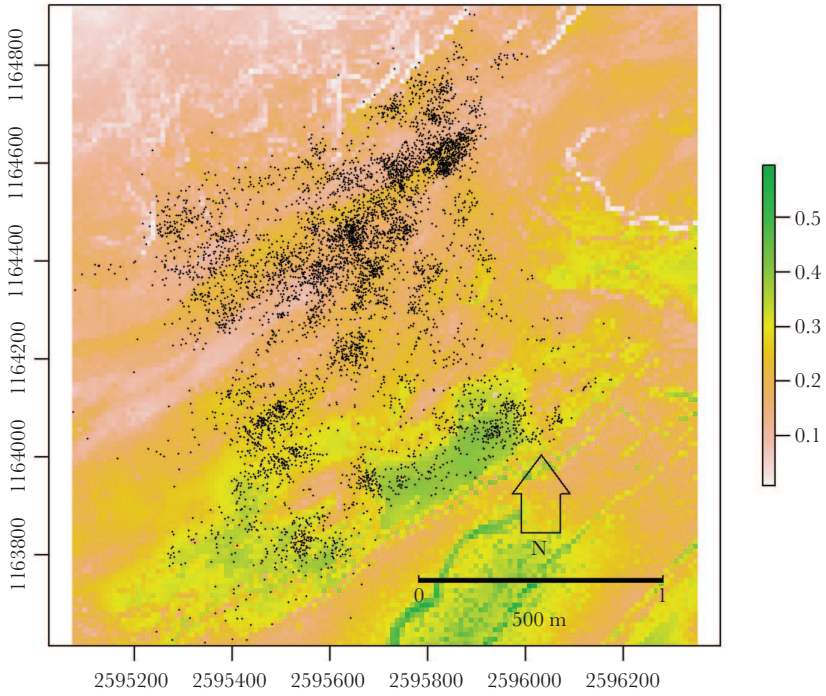

Figure 2
Map of chronic lynx predation risk during a winter night for the home range of a radio-collared roe deer. Predation risk was derived from a lynx habitat selection model. Because this predation risk model was temporally dynamic we fixed time and season at a random value for the graphical representation here. The white-green gradient indicates variation in chronic predation risk. Black dots indicate roe deer locations of individual UZH_205.

perception of predator cues by prey is multimodal and includes visual, acoustic and chemical processes (Weissburg et al. 2014). However, the factors affecting the distances over which predation risk is perceived and for how long are still not well understood. Several studies have reported that the reactive response of ungulate prey to the immediate presence of large predators such as wolves or lions can last for several days and carry over several kilometers (e.g., Valeix et al. 2009: 2 km and 24 h, Periquet et al. 2012: ~2 km, Latombe et al. 2014: 4.7 km and 10 days, Basille et al. 2015: 2.9 km and 15 days). The strongest response has been reported within the first 24 h after predators and prey approached each other within 1 km (Middleton et al. 2013). We thus defined acute predation risk as encounters between collared lynx and collared deer where a lynx was present within 1km of a deer over the past 24 h. This definition of encounter only refers to spatial and temporal proximity and does not guarantee that predator and prey sensed each other. However, given the high mobility of predators and prey in relation to GPS fix intervals it is likely that in many instances the true proximities between predators and prey was much closer than recorded at times of GPS fix locations (Creel et al. 2013). For each roe deer, we counted the total number of recorded encounters and calculated the encounter frequency per individual deer. Note that both conditions (i.e., 24 h and 1 km) had to be met in order for a location to count toward an encounter. Thus, when a deer moved away more than 1 km from where a lynx had passed within the past 24 h we assumed the response of the deer stopped as it no longer perceived the lynx according to our definition of acute predation risk. This is a conservative approach as deer may uphold a reactive response even after they have ceased to perceive a predator cue (e.g., Latombe et al. 2014; Basille et al. 2015). We chose this approach to capture the time period when deer were most likely to engage in the strongest reactive response. To count the number of individual encounters only incidences that were more than 24 h apart were considered as separate encounters. Not all lynx in the study area were collared and therefore some of the nonencounter locations would in reality be encounter locations with unmarked lynx (e.g., only 4 of 10 roe deer killed by a lynx were killed by a collared lynx). For this reason, the calculated encounter frequency in this study will be an underestimate of the true encounter frequency, and the observed reactive response may in fact be greater than what we measured in this study.

Modeling the proactive and reactive response of roe deer to risky places and risky times

We tested the response of deer to risky places and risky times using step selection functions (SSF). We first outline the statistical approach and then introduce important habitat variables generally involved in roe deer habitat selection. We then detail how we tested the proactive and reactive response of roe deer to chronic and acute lynx predation risk with respect to predictions 1–3 outlined in the introduction. We restricted our analyses to 49 deer (301,103 locations) for which we had identified encounters with 11 lynx according to the criteria described above.

Separating animal paths into steps

For the habitat selection analysis, animal paths were broken down into successive steps. Each step was characterized by the step length (the straight-line segment between 2 successive GPS locations) and the turning angle (the angle between the previous and current step). Each step was assigned habitat variables and the chronic predation risk value found at the end of the step (see "Chronic predation risk" above). Encounters between lynx and roe deer (i.e., acute risk) were assigned to the beginning of a step in order to measure the response of the deer to the encounter (see next section for details).

Following this approach, we calculated for each deer step the time and distance to all lynx locations that fell within the constraints outlined above. If more than one lynx location fell within 1km and 24 h, only the most recent location was kept.

Independence of movements of collared roe deer

Several collared roe deer formed transient coalitions for extended time periods. Hence, in the habitat selection analysis outlined in the following section we could not assume independence of movements between all deer at all times. To identify deer social groups we calculated the distance between concurrent locations of all deer with overlapping 100% MCP (Fortin et al. 2005). Deer movements were considered independent, when animals were further apart than 50 m and dependent otherwise. Roughly 12% of all steps were paired steps. We accounted for nonindependence of paired steps between deer by randomly selecting one step per pair and removing the other. Robust variances were calculated from this reduced dataset (see SSF modeling).

SSF modeling

The proactive and reactive response of roe deer to chronic and acute lynx predation risk was analyzed using SSF (Fortin et al. 2005). Each realized step of the final datasets was paired with 10 alternative random steps. Random step lengths and turning angles were drawn in pairs from the empirical distributions in the data. These paired realized and random steps represent case–control data and were analyzed using conditional logistic regression (Thurfjell 2014).

Successive steps of the same animal in SSF cannot be considered independent (reviewed in Fieberg et al. 2010). We used the autocorrelation in the deviance residuals to determine the lag after which steps could be considered independent (Fortin et al. 2005). Autocorrelation in the deviance residuals was considered negligible when values dropped below 0.1 and robust variances for regression coefficients were estimated by creating independent clusters of correlated steps as described in Forester et al. (2009).

To test the fit of the models, we performed cross validations for case–control designs as described in Fortin et al. (2009). Instead of dividing the data randomly, we removed groups of 5 individuals as test datasets and built the SSF on the remaining deer (see Gehr et al. 2017b for more details). Average spearman rank correlations (r_s) over 100 trials are reported with associated 95% confidence intervals. High r_s values are indicative of a good model fit.

All continuous covariates were standardized (mean of 0 and SD of 1). Variance inflation factors (VIF) were used to test for multicollinearities among all model covariates. VIF-values larger than 2 could all be attributed to the inclusion of interactions and power transformations (max VIF was 4.6 for the altitude-season interaction). Thus, multicollinearity was a minor issue in our models (Zuur et al. 2009).

Habitat variables

Habitat variables known to be important for roe deer were included in the SSF. Roe deer occur at high densities in fragmented cultivated landscapes, where they are closely associated with forest edges at the interface of open habitat and forest (Danilkin and Hewison 1996). Open habitats (e.g., meadows and crop fields) provide rich feeding opportunities for deer but are associated with high human disturbance, whereas forests may provide some food but also cover and refuge (e.g., Hewison et al. 2001; Padie et al. 2015). Therefore, open habitat was included as a dummy variable with 1 = open and 0 = forest. We further included distance to the closest forest edge to account for the fact that deer may evaluate human-related risk in the open depending on the distance to cover but also because edge habitat may be associated with increased predation risk from lynx (e.g., Podgorski et al. 2008) but also. We quantified human proximity using an index of building density and distance to the closest road, 2 parameters that have been shown to induce avoidance behavior in roe deer (Coulon et al. 2008; Gehr et al. 2017b). This human disturbance index was calculated as the difference between the scaled house density and road distance. Hence, a large value of this index represents areas with a high density of houses and roads close by. Furthermore, altitude and slope were included, since climate varies with altitude and steep slopes may serve as a refuge for roe deer (Lone et al. 2014). For both altitude and slope, a quadratic term was included to allow for nonlinear effects of these habitat variables. Finally, southern exposed slopes (dummy variable with 1 = southern exposed slope and 0 = all other directions) may be preferred by ungulates during winter because this is where snow cover first disappears (e.g., Plank 2013).

Temporal variables

Habitat selection of roe deer differs between day and night due to differences in human activity and predation risk (Hewison et al. 2001; Padie et al. 2015). Thus, separate SSF models were constructed for day and night (sun angle >0=day, night otherwise). Moreover, as snow cover is known to affect habitat selection as well as predation risk (Mysterud et al. 1999), we defined the beginning of November until the end of April as the winter season, when snow typically covers the ground, and the beginning of May until the end of October as the summer season (note that 11 of 49 deer showed seasonal migrations between summer and winter ranges but we did not expect this to interfere with our analyses, because our models captured these seasonal changes in habitat). Because season is constant across a stratum of used and associated random steps, and because conditional logistic regression does not allow to fit main effects for predictors that are constant within stratum, season was only included in interaction with habitat variables in the SSF model.

We did not expect selection of all habitat covariates to depend on season. Selection of slope and distance to forest was expected to mainly depend on human proximity, which itself mostly follows circadian rather than seasonal fluctuations. Hence, no interaction terms for slope, distance to forest, and human proximity with season were included.

Response to risky places and risky times

Chronic and acute lynx predation risks were added as covariates in the SSF to model the proactive and reactive response of roe deer to risky places and risky times. The proactive response of deer to risky places was tested with the main effect and a quadratic term of chronic lynx predation risk (*prediction 1*). To test *prediction 2*, an interaction term was included between chronic predation risk and acute predation risk to test whether deer avoided chronic risk areas more during risky times when a lynx was present (reactive response). Because associated realized and random steps shared the same acute predation risk (0 = no encounter in the past 24 h within 1 km, 1 = encounter in the past 24 h within 1 km) no main effect for encounter could be included in the models. Moreover, deer home ranges in our study area are ca. 5 km^2, which makes it difficult to detect the immediate reaction of a deer to an encounter at the considered scale (1 km within 24 h). For *prediction 3* we tested whether

roe deer reduced their movement rates during acute predation risk (a reactive response to risky times) by including an interaction term between encounter and step length (e.g., Basille et al. 2015). Finally, we included interaction terms between season and chronic predation risk and squared chronic predation risk, respectively, to test whether avoidance of risky places differs between winter and summer.

Impact of nonconsumptive effects on roe deer survival

To test whether nonconsumptive effects of lynx can affect deer survival in accordance with *prediction 4*, we employed Cox proportional hazards models using mortality data from collared deer. In the following, we first describe the mortality data and then the proportional hazards models.

Mortality data

Collars were equipped with a mortality switch (triggered after 4–6 h of inactivity) that allowed us to assess time and cause of death. Mortality signals were checked every other day. Carcasses of natural mortalities other than lynx predation were brought to the Centre for Fish and Wildlife Health at the University of Bern to determine cause of death. Deer killed by lynx were not removed from the site to avoid increasing the hunting efforts of lynx, which could result from kill removal. Hunted animals were reported by the hunters. Mortalities (n = 40) were separated into lynx predation (n = 10, 25%) and all other sources of mortality (n = 30, 75%). The latter category included hunting (n = 12 or 30% of all mortalities, including 2 poached deer), dog predation (n = 2, 5%), disease and starvation (n = 7, 17.5%), road kills (n = 2, 5%), and unknown causes (n = 7, 17.5%). Unknown mortalities were unlikely due to lynx since lynx kills are easily identified when found within 1–2 days. Hence, we included unknown mortalities in our analyses. However, results did not change when these mortalities were excluded.

Cox proportional hazards modeling

We used Cox proportional hazards models to quantify the degree to which deer exposed to higher chronic lynx predation risk suffered from higher nonlynx predation-related mortality. Thus we calculated for each deer the mean chronic predation risk (see "Chronic predation risk") over all used and random locations as a measure of predation risk exposure in the model. To provide a perspective on the relative importance of lynx nonconsumptive effects on deer mortality, mean human proximity (see "Habitat variables") was included as an additional explanatory variable. We thus assumed that human proximity may influence nonlynx mortality directly (e.g., through increased risk of road accidents, dog predation, or human hunting) or indirectly, similar to nonconsumptive effects (e.g., through chronic stress affecting mortalities such as disease or starvation). Because altitude positively correlated with chronic predation risk (r = 0.69) and negatively with human proximity (r = −0.42), we also included mean altitude per deer as a third covariate in the models to account for multicollinearity in the model. We built 3 candidate models considering chronic predation risk and human proximity separately or in combination with each other and selected the most appropriate model explaining survival patterns using AIC scores (Burnham and Anderson 2002). Altitude was kept as a predictor in all 3 models due to the correlation between altitude and predation risk. We used a staggered entry design using daily encounter histories. The mortality data from all 65 deer were parametrized as follows: all mortalities excluding mortalities from lynx predation were assigned as mortalities (30 mortalities; see "Mortality data"), whereas lynx kills and animals alive at the end of the study were entered as censored observations. The proportional hazard assumption was tested using scaled Schoenfeld residuals (cox.zph function, Fox 2003). Influential points were identified by plotting transformed score residuals against individual model predictors (Therneau and Grambsch 2000).

For graphical presentation (Figure 5), we reformulated the Cox model as a Poisson regression model (Therneau and Grambsch 2000) and created added variable plots (Fox and Weisberg 2011) for predation risk and human proximity while accounting for the effects of all other predictors in the model. This reformulation was necessary because added variable plots are not straightforward to implement in Cox models (Therneau and Grambsch 2000).

All statistical analyses were conducted using R version 3.1.1 (R Core Team 2014).

RESULTS

The mean chronic predation risk (scaled between 0 and 1) at night for random locations within lynx home ranges was 0.25 compared to 0.39 for night locations of lynx ($t_{6410.7}$ = 41.3; P < 0.001) and 0.29 for kill sites ($t_{200.04}$ = 2.9; P = 0.004), respectively. Thus, our lynx model is a useful measure of lynx encounter probability for roe deer, but lynx are not killing deer where lynx spend most of their time. Pronounced variation in exposure to mean chronic predation risk was found among collared deer. The lowest and highest mean chronic predation risk of individual deer differed by a factor 7 and ranged between 0.05 and 0.37. The average mean chronic predation risk for all deer was 0.17, showing that deer on average clearly avoid chronic predation risk (Table 1).

Table 1

Summary statistics of important spatial and temporal parameters of lynx and deer movement

	First quartile	Median	Third quartile
Lynx			
Home range size (km^2)	121	134	298
Step length (3 h steps), daytime (m)	31	194	743
Step length (3 h steps), nighttime (m)	26	250	1069
Chronic predation risk	0.24	0.34	0.48
Roe deer			
Home range size (km^2)	2.63	4.81	10.43
Step length (2 h steps), no reactive response at daytime (m)	30	69	158
Step length (2 h steps), during reactive response at daytime (m)	29	67	154
Step length (2 h steps), no reactive response at nighttime (m)	24	60	151
Step length (2 h steps), during reactive response at nighttime (m)	23	56	139
Mean chronic predation risk per deer (scaled 0–1)	0.12	0.17	0.23
Encounter frequency per deer (interval in days)	41	56	120

Summary statistics are reported separately for lynx and roe deer. Home range areas were calculated using the 100% minimum convex polygons. Step lengths are reported for day and night separately. For deer, step lengths are further separated into steps in the absence of a reactive response and steps during a reactive response. The chronic predation risk is derived from a lynx habitat model. The encounter frequency indicates the number of days between encounters calculated for each deer separately.

We identified a total of 465 encounters between 11 lynx and 49 deer. The encounter frequency (number of days between encounters) strongly differed among deer but was highly left skewed. The deer with the highest encounter frequency experienced a lynx encounter every 13 days, whereas the median frequency was 56 days. Roughly 2% of all deer steps (6672 steps) were associated with acute predation risk during which a collared lynx was closer than 1km within the past 24 h. During the closest encounter a lynx came within 21 m of a deer with a time delay of 11 h (in reality predator and prey may have come much closer to each other in between GPS fixes). During the closest real time encounter (time delay = 0) a lynx came within 180 m of a collared deer. The average encounter distance was 712 m with an average time delay of 10 h. Important spatial and temporal parameters of deer and lynx movements are summarized in Table 1.

Proactive and reactive response of roe deer to risky places and risky times

The SSF model for the night revealed no autocorrelation in the deviance residuals and hence correcting model standard errors was unnecessary (Supplementary Appendix S1: Figure S1b). In the day model, autocorrelations persisted for 48 h and we calculated robust standard errors accordingly (Figure S1a). Cross-validation results for the day and night SSF models differed significantly from the null model of random space use and indicated good model fit in both cases (mean $r_{s\text{-DAY-used}}$ = 0.999 vs. mean $r_{s\text{-DAY-random}}$ = 0.293; mean $r_{s\text{-NIGHT-used}}$ = 0.895 vs. mean $r_{s\text{-NIGHT-random}}$ = 0.307). In general, habitat selection of roe deer differed markedly between day and night as well as between summer and winter (Table 2). During the day roe deer strongly avoided open habitat and human proximity. During the night deer spent more time in the open closer to human features and also further away from the forest edge. Furthermore, roe deer preferred less steep slopes during the night than during the day.

In summer, deer spent more time in the open than during winter and this pattern was particularly strong at night (Table 2). In contrast, roe deer preferred southern exposed slopes during winter but not during summer. Finally, roe deer seemed to choose intermediate altitudes in winter during the day, whereas at all other times roe deer preferred low altitudes.

Response to risky places and risky times

The proactive response of roe deer to chronic lynx predation risk was nonlinear and strongly dependent on the time of day and season. During the day, there was weak positive selection for low to intermediate predation risk but strong avoidance of high chronic predation risk as expected from *prediction 1* (Table 2, Figure 3a). This was true for both winter and summer. At night, on the other hand, deer strongly avoided chronic predation risk during summer but seemed to select for intermediate to high risk in winter (Figure 3b).

In addition to a proactive response to chronic lynx predation risk, roe deer also showed reactive responses to risky times under acute predation risk: As expected from *prediction 2*, roe deer avoided chronic predation risk more (during the day) or selected it less (at night) in situations of acute predation risk, than when no lynx was in the vicinity (Figure 4 and Table 2). The reactive response was weaker than the proactive response and weaker during the day than at night. The 95% confidence limits for the interaction term between the proactive and reactive response in the day model slightly overlapped with 0 (Table 2). In addition to an increase in avoidance of chronic predation risk, roe deer also reduced their movement rates during acute predation risk, in line with *prediction 3*. This reduction in movement rates, however, was only evident during the night and the effect size was small (Step length:Acute predation risk interaction in Table 2, summarized in Table 1).

Table 2

Model output of the 2 step selection function models for day and night

	SSF day					SSF night			
Variables	β	Model_se	Robust_se	Lower CI	Upper CI	B	Model_se	Lower CI	Upper CI
Open habitat	−0.519	0.017	0.047	−0.611	−0.427	−0.147	0.011	−0.169	−0.124
Open habitat:Season	−0.027	0.021	0.055	−0.135	0.081	0.542	0.016	0.510	0.574
Human proximity	−0.203	0.005	0.009	−0.220	−0.185	−0.059	0.005	−0.068	−0.049
Southern exposition	0.131	0.013	0.026	0.081	0.182	0.181	0.012	0.157	0.206
Southern exp:Season	−0.235	0.017	0.032	−0.298	−0.171	−0.180	0.017	−0.214	−0.147
Distance to edge	−0.572	0.006	0.017	−0.604	−0.539	0.036	0.004	0.027	0.044
Slope	0.144	0.005	0.010	0.124	0.163	−0.044	0.005	−0.053	−0.035
Slope sq.	−0.150	0.003	0.006	−0.161	−0.139	−0.118	0.003	−0.125	−0.112
Altitude	−0.020	0.026	0.044	−0.107	0.067	−1.140	0.026	−1.191	−1.088
Altitude sq.	−0.111	0.009	0.015	−0.140	−0.081	0.003	0.009	−0.015	0.021
Altitude:Season	−0.273	0.033	0.056	−0.383	−0.162	0.571	0.038	0.496	0.646
Step length	0.030	0.003	0.007	0.016	0.044	0.056	0.003	0.051	0.062
Step length:Acute PR	0.015	0.019	0.038	−0.059	0.089	−0.064	0.020	−0.103	−0.024
Chronic PR	0.135	0.016	0.034	0.067	0.202	0.409	0.016	0.377	0.440
Chronic PR sq.	−0.078	0.005	0.010	−0.097	−0.059	−0.072	0.004	−0.080	−0.065
Chronic PR:Season	−0.030	0.021	0.046	−0.121	0.061	−0.540	0.030	−0.599	−0.481
Chronic PR sq:Season	0.023	0.006	0.013	−0.002	0.049	0.065	0.009	0.048	0.083
Chronic PR:Acute PR	−0.090	0.028	0.050	−0.188	0.007	−0.108	0.036	−0.178	−0.037

Model coefficients together with standard errors and 95% confidence intervals are shown. For the day model, the model standard errors are reported together with the robust standard errors. For the night model, the model standard errors were used to calculate confidence intervals as there was no residual autocorrelation in the deviance residuals of the model. Habitat selection and risk avoidance of roe deer differed markedly between day and night as well as between summer and winter. The response to acute predation risk was more pronounced during night than day. In general, roe deer avoided chronic predation risk more and reduced their movements during acute predation risk. Open habitat was a dummy variable (forest = 0 and open habitat = 1) whereas for season winter was taken as the reference category.
PR, predation risk.

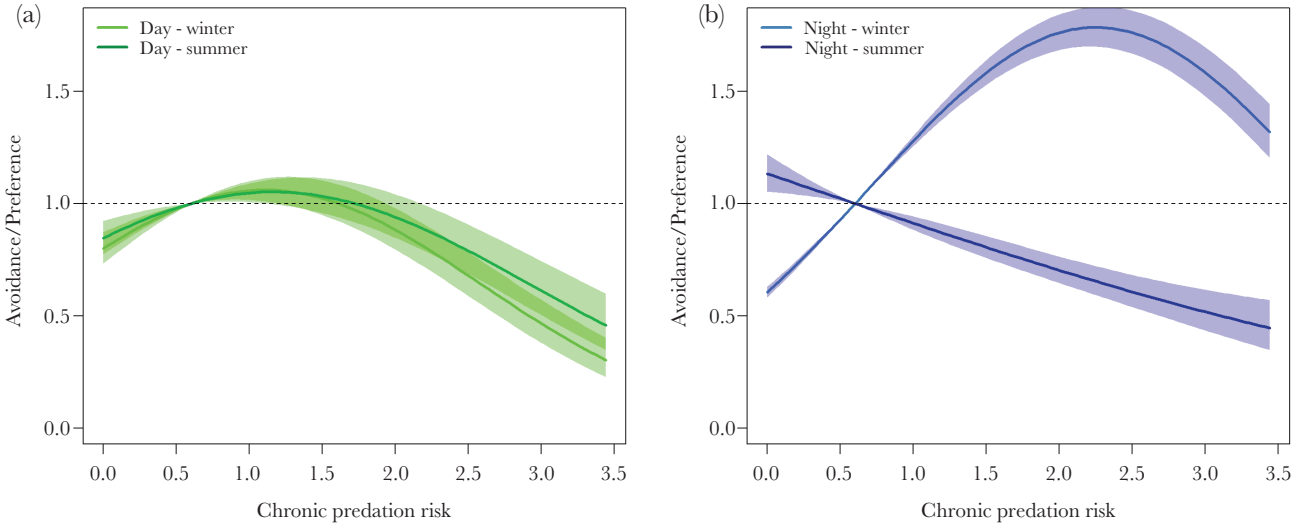

Figure 3
Selection coefficients of chronic predation risk during day (a; green) and night (b; blue), in summer and winter. Selection curves together with the 95%-pointwise confidence bands are shown. The dashed horizontal line at y = 1 indicates no selection. During the day, there was weak positive selection for low to intermediate predation risk but strong avoidance of high chronic predation risk irrespective of season. At night, on the other hand, deer strongly avoided chronic predation risk during summer but seemed to select for intermediate to high risk in winter.

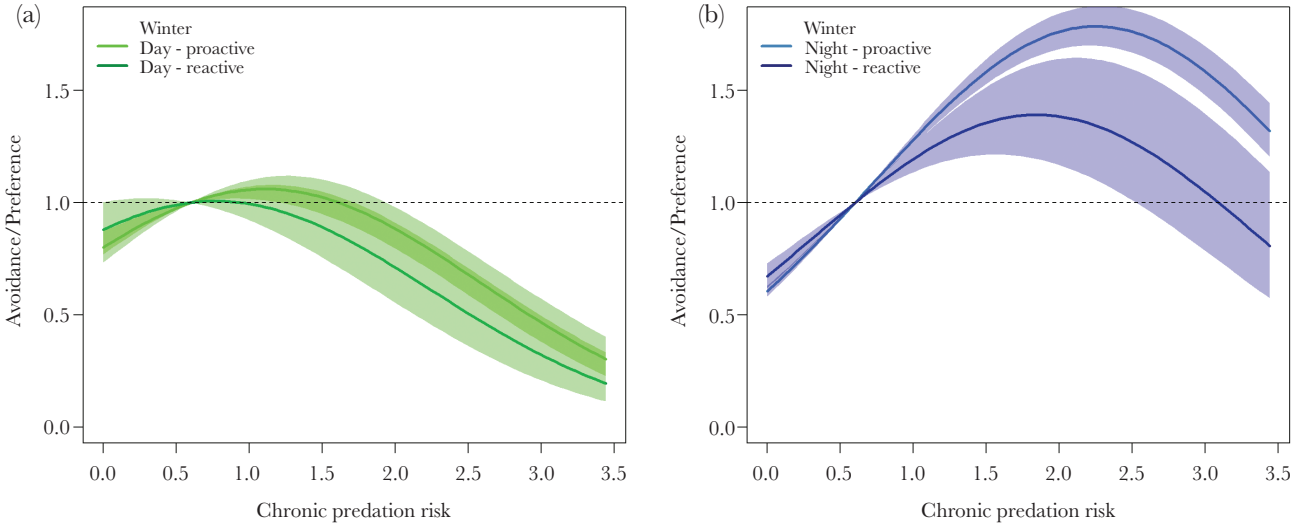

Figure 4
Selection coefficients of chronic predation risk in the absence of lynx compared to selection during acute predation risk (acute PR) when a lynx was close by. Results from the day model are shown in green (a) and from the night model in blue (b). Selection curves together with the 95%-pointwise confidence bands are shown. The dashed horizontal line at y = 1 indicates no selection. Roe deer avoided chronic predation risk more (during the day) or selected it less (at night) in situations of acute predation risk, than when no lynx was in the vicinity.

Impact of nonconsumptive effects on roe deer survival

The proportional hazards model with the lowest AIC score included all 3 predictors: mean human proximity, mean altitude and mean chronic predation risk (Table 3). Inspection of the Schoenfeld residuals indicated no violation of the proportional hazard assumption. Removing putatively influential points did not change the results of the model. As expected from *prediction 4* we found evidence that nonconsumptive effects were strong enough to translate into survival costs. Roe deer living in areas of high chronic predation risk (risky places) experienced increased nonlynx-related mortality (hazard ratio = 4.25, $P < 0.001$, Table 4 and Figure 5a).

Table 3
Model selection among the 3 Cox proportional hazards models tested

Model	LL	K	AICc	ΔAICc	ω
Chronic PR+Hum. Prox+Altitude	−101.260	3	208.914	0.000	0.970
Chronic PR+Altitude	−106.174	2	216.541	7.627	0.021
Hum. Prox+Altitude	−107.091	2	218.376	9.462	0.009

The 3 models quantified the effect of human proximity and mean chronic predation risk (chronic PR) on the hazard ratio of roe deer mortality while accounting for mean altitude. The best model included all 3 predictors.

Living at higher altitudes showed a tendency to reduce the hazard of dying for roe deer (hazard ratio = 0.708, $P = 0.25$), whereas proximity to humans was associated with increased mortality risk (hazard ratio = 2.43, $P = 0.004$, Table 4 and Figure 5b). The comparison of the nonconsumptive effects of lynx with the effects of human proximity showed that a one unit increase in chronic predation risk increased the risk of mortality 75% more than a corresponding increase in human proximity (4.25/2.43).

DISCUSSION

In this study, we used GPS location data from independent data sets of simultaneously collared lynx and roe deer to quantify how an ungulate prey responds to the long-term, chronic predation risk of a large predator and how this antipredator behavior changes during acute predation risk when the predator is in the vicinity. Furthermore, we tested whether the predator-induced behavioral changes translate into survival costs. We found that roe deer responded to both, risky places (chronic predation risk) and risky times (acute predation risk) very dynamically depending on the spatial and temporal context (e.g., proximity of humans or season). We provide evidence that these behavioral antipredator responses of roe deer can be strong enough to affect deer survival and show that deer mortality in this study was more sensitive to variation in the nonconsumptive effects of lynx than to variation in the effects of human proximity. In the following, we discuss our findings in light of the 4 predictions we made in the introduction:

Table 4

Model output for the best-fitting Cox proportional hazards model

Variables	β	exp(β)	Lower CI	Upper CI
Chronic predation risk	1.446	4.246	1.891	9.530
Human proximity	0.889	2.432	1.335	4.432
Altitude	−0.345	0.708	0.393	1.275

The model tested for an effect of nonconsumptive effects of lynx predation and human proximity on deer mortality risk. Model coefficients are reported together with the hazard ratios (HR = exp(β)) and their 95% confidence intervals. HR > 1 indicates an increase in risk whereas a HR < 1 indicates a reduced risk relative to the baseline hazard. Nonconsumptive effects had 75% stronger impact on nonlynx-related roe deer mortality than human proximity (4.25/2.43). Altitude was negatively associated with mortality although the effect was not significant at the 5% level.

Roe deer proactively avoid areas of high chronic lynx predation risk according to the risky places hypothesis

The proactive response of roe deer to chronic predation risk by lynx only partly followed our first prediction because, depending on season and time of day, deer sometimes avoided but also sometimes positively selected chronic predation risk (Figure 3). The joint distribution of predator and prey is the result of a "shell game" in which predators try to find their prey whereas prey intend to be unpredictable for the predator (Mitchell and Lima 2002). This results in the prediction that predators will aggregate in areas where the resources of prey are abundant while the prey will have to tradeoff between resource acquisition and predation avoidance. How prey will behave given this tradeoff will depend on internal (e.g., reproductive state or body condition) and external (e.g., food abundance or daylight) constraints, which are subject to temporal and seasonal variation (Sih 2005). During the day, human activity is high whereas lynx activity is low. This explains the strong avoidance of open habitat (Table 2), which is where human disturbance is highest during the day. The low activity of lynx during the day may also explain why roe deer respond generally less to chronic lynx predation risks during the day than during the night (Figure 3). During summer nights, when lynx are active but humans are not, roe deer strongly avoid chronic predation risk by lynx and

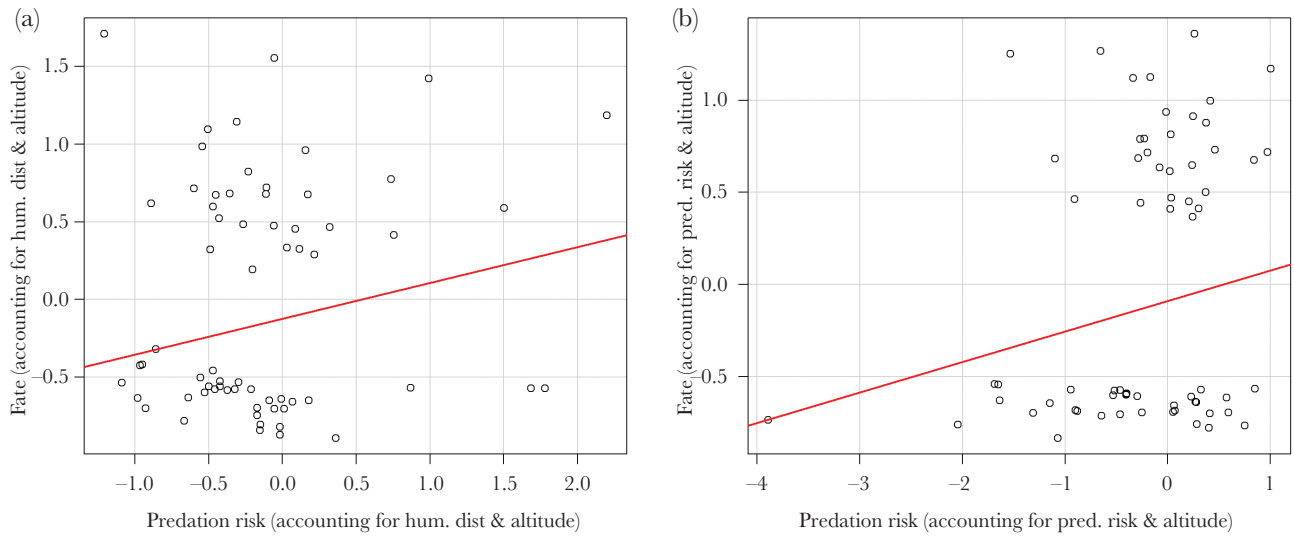

Figure 5

Added variable plots showing the effects of (a) chronic predation risk and (b) human proximity on the hazard rates estimated by the Cox proportional hazard model. For graphical representation we reformulated the model as a Poisson regression (Therneau and Grambsch 2000). The added variable plot shows the effect of a predictor variable (on the link scale, here the log function for a Poisson regression) on the response (i.e., fate = death vs. alive/censored) while accounting for the effects of all other predictors in the model (i.e., human proximity and altitude for chronic predation risk and chronic predation risk and altitude for human proximity). Both mean chronic predation risk (hazard ratio = 4.25, $P < 0.001$) as well as human proximity (hazard ratio = 2.43, $P = 0.004$) were associated with higher nonlynx-related mortality.

spend most of the time in the open further away from forest edges thereby reducing the risk of encountering lynx. This held true even after accounting for higher food availability in open habitats during spring and summer (Danilkin and Hewison 1996) by including open habitat and its interaction with season in the models. This pattern is reversed in winter, probably because roe deer are constrained by cold temperatures and dense snow cover which forces them to stay inside the forest even at night (Mysterud et al. 1999). Thus, in winter roe deer are forced to accept higher levels of lynx predation risk at night due to severe weather conditions and low accessibility of food, a situation also reported in other recent studies (Ratikainen et al. 2007; Lone et al. 2016). This may increase stress and contribute to the strong nonconsumptive effects reported here. Overall, our results show that the distribution of predators and prey is the result of a "behavioral response race" in which both players have to trade off between internal and external constraints, when making decisions on habitat selection or risk avoidance (Sih 2005). Depending on these tradeoffs in predator and prey, the outcome of the race will be different (i.e., positive or negative association between predator and prey), and it will be subject to temporal and seasonal fluctuations. In this sense, our findings emphasize the importance of incorporating the temporal dimension in analyses of predator–prey interactions (e.g., Middleton et al. 2013; Basille et al. 2015). Our analyses show, that lynx do not necessarily kill deer where lynx spend most of their time and we do not currently know the indirect cues that roe deer use to assess chronic predation risk (but see Kuijper et al. 2013). Thus, our measure of chronic predation risk may deviate from the landscape of fear determining the foraging costs of predation for deer. However, our analyses have shown that deer do proactively respond to the risk of encountering a predator which negatively affects their fitness even though there may be many other factors affecting proactive risk avoidance (e.g., vulnerability of prey, density-dependent habitat selection, habitat visibility, etc.). A better understanding of these factors is necessary to better quantify the indirect costs of predation.

Roe deer increase their avoidance of high risk areas during a reactive response (i.e., under acute predation risk) according to the risky times hypothesis

Roe deer altered their antipredator behavior in situations of acute predation risk in that they moved to safer habitats when lynx were in the vicinity (Figure 4). Even though the effect was not very strong, these results confirm other studies that found prey moving to safer habitat as a reactive response to predator presence (Valeix et al. 2009; Thaker et al. 2012; Creel et al. 2014). By adjusting antipredator behavior flexibly to predator presence, prey species can avoid maintaining potentially costly antipredator behavior during times when no predator is around. Such flexible antipredator behavior may be a general feature of many herbivores (Creel et al. 2014). The reason why the response of deer to predator presence reported here was not stronger, may be partly due to the fact that our measure of acute predation risk was associated with uncertainty and partly due to the imperfect knowledge of deer about predator presence.

Roe deer reduce their movement rates during acute predation risk according to the risky times hypothesis

In addition to avoiding areas of higher encounter probabilities during acute predation risk, roe deer also showed a weak reduction in their movement rates, but only at night (Tables 1 and 3). Activity reduction under acute predation risk has been shown in different small mammal species and has been explained with reduced detection probability from predators (e.g., Kotler et al. 1992; Borowski and Owadowska 2010). Activity reduction in roe deer in response to acute predation risk by lynx is likely to serve a similar purpose. Alternatively, the reduced movement rates we observed may simply be a consequence of roe deer not retreating into the risky forest for resting when a lynx is nearby, but instead choosing to stay in the open refuge habitat for both resting and feeding. Overall, the results from prediction 2 and 3 together suggest that plasticity in the response to risky places depending on predator presence or absence may allow prey species to capitalize on resources in high risk habitat during times of predator absence.

Roe deer living in areas of high predation risk suffer from reduced survival due to nonconsumptive effects

The importance of nonconsumptive effects for prey population dynamics has been shown in different taxa (Preisser et al. 2005), yet examples from large terrestrial mammal systems are rare (Creel et al. 2013). Our results provide evidence that roe deer living in areas of high chronic predation risk (risky places) suffer from increased non-lynx predation-related mortality as a result of strong nonconsumptive effects (Table 4). Through the combined effects of hunting and other direct effects (road kills and dog predation), humans clearly pose the biggest mortality risk for roe deer in our study site (16 of 40 mortalities or 40% of total recorded deaths). After humans, lynx are the second most important direct cause of mortality for roe deer. This not only holds for our study site (10 mortalities or 25%), but also elsewhere where the 2 species co-occur, and different studies have shown that lynx predation strongly impacts roe deer population dynamics (Melis et al. 2009; Nilsen et al. 2009). In this context, the median encounter frequency of 56 days that we observed does not seem very high. However, not all lynx in the study area were monitored at all times. Moreover, the highest observed encounter frequency of 13 days shows that this number can be considerably higher and may result in significant energetic costs for a deer if sustained over an extended period of time. Such high predation pressure is expected to increase the contribution of nonconsumptive effects to total predator impact relative to the consumptive effects (Creel et al. 2011) and may explain the strong effects on deer survival found here.

Roe deer mortality in this study was more sensitive to variation in the nonconsumptive effects of lynx than to variation in the effects of human proximity. These findings highlight that the tradeoff prey species are facing between avoiding large predators and human-related risks in human dominated landscapes may have far reaching consequences for prey demography that go beyond the direct numeric effects of these opposing risk factors (e.g., Gehr et al. 2017b). Studies have shown prey to use humans as shields against natural predators (e.g., Berger 2007 showing elk to shift birth sites closer to roads in order to avoid traffic averse bears). Our findings indicate that if roe deer exhibited such behavioral responses to lynx predation risk by moving closer to humans, they would suffer from increased mortality due to the proximity to humans (e.g., hunting, road kills, etc.). Further studies will be necessary to confirm our results and to investigate potentially maladaptive behavior that might render proximity to humans into ecological traps (Gilroy and Sutherland 2007).

As with all correlational studies, we cannot rule out that the observed reduction in survival was caused by some unmeasured variable, such as

habitat quality. However, since habitat quality generally decreases with altitude and we found a positive effect of altitude on survival, our results are not consistent with an undetected effect of habitat quality causing the observed survival patterns. Furthermore, we do not know whether the observed reduction in survival in roe deer is related to a reduction in foraging rate and quality, or due to a chronic stress response as a result of sustained 'psychological` stress (Christianson and Creel 2010; Creel et al. 2011; Clinchy et al. 2013). Quantifying the impacts of predation on foraging (e.g., by measuring giving-up densities—Brown et al. 1992) and a comparison of resource availability and actual habitat use would be necessary to identify the proximate causes of the observed reduction in survival. We encourage further studies that include measures of habitat quality in other systems with different environmental context to confirm our results for large terrestrial vertebrate predator–prey systems.

CONCLUSIONS

Not many studies have investigated both proactive and reactive responses of prey to risky places and risky times, and very few studies have quantified how nonconsumptive effects translate into fitness costs in large mammals (but see MacLeod et al. 2017). Wolves in North America have been a major focus of such research, yet the evidence in wolves remains controversial as some studies find strong nonconsumptive effects (Creel et al. 2007; Christianson and Creel 2010) whereas others do not (Middleton et al. 2013). The findings reported here suggest that nonconsumptive effects, strong enough to affect prey survival, can occur in large mammal predator–prey systems. However the extent to which environmental factors such as habitat composition or the occurrence of other risk factors such as human presence interact with nonconsumptive effects remains to be shown (Creel 2011). Our findings contribute to the development of a conceptual framework explaining how predators affect prey populations in large terrestrial predator–prey systems and call for more work on the interaction between human disturbance and nonconsumptive effects in these systems.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Gehr et al. (2018).

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